

New Information on Morphology, Stratigraphy, and Paleoclimate
Implications of the Eocene Brackish-Marine Gastropod *Loxotrema turritum*
Gabb, 1868, from the West Coast of the United States

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Abstract. New morphologic information about the aperture of the brackish-marine Eocene gastropod *Loxotrema turritum* Gabb, 1868, allows for reassignment of this species from family Thiaridae to family Melanopsidae and shows that *L. turritum* is most closely related to the melanopsid *Faunus ater* Linnaeus, 1758, found today in the fully tropical Indo-West Pacific region near the mouths of rivers. New stratigraphic and geographic data show that the earliest record of *L. turritum* is in lowermost Eocene ("Meganos Stage") rocks in northern California, and that the species was most widespread during the middle lower Eocene ("Capay Stage") when it ranged from southern California to as far north as Crescent Bay, Washington. Most of these "Capay Stage" specimens underwent downslope postmortem transport, most likely from deltaic areas, into deeper waters and became mixed with shallow-marine mollusks. The "Domengine Stage" record of this species is known only from California. From the middle part of this stage (lowermost middle Eocene) through the end of the geologic range of this species in the lower part of the "Tejon Stage" (lower middle Eocene), *L. turritum* lived in brackish-marine lagoons or bays within deltaic complexes in southern California. The last records of this species help confirm data from other disciplines that during the early middle Eocene there was a climate change from humid to drier conditions.

INTRODUCTION

The brackish-marine gastropod *Loxotrema turritum* Gabb, 1868, the only known species of genus *Loxotrema* Gabb, 1868, is confined to lower and lower middle Eocene rocks on the west coast of the United States. This article, which represents the first detailed study of any Eocene brackish-marine mollusk from the west coast of the United States, contains a thorough review of the stratigraphic occurrences and inferred depositional environments of this species. In addition, it contains the first discussion of the paleoclimatic implications of this species.

Loxotrema turritum is very distinctive due to its tabulate whorls and large cylindrical body whorl, but specimens are prone to poor preservation of the outer lip and the anterior end of the aperture, as evidenced by nearly all the published illustrations of this species. These features, which are critical in determining familial assignment, have not been used before by other workers, who, on the basis of general morphology, traditionally placed *Loxotrema* in the family Thiaridae. I examined nearly 300 specimens of *L. turritum*, most of which are stored at several museums on the west coast. I found only a single individual that shows the entire aperture and only two individuals that show some indication of protoconch morphology. This new morphological information reveals that *L. turritum* is most closely related to the extant melanopsid *Faunus ater* Linnaeus, 1758.

While examining museum collections, I found new stratigraphic and geographic occurrences of *L. turritum*. The known geologic range of this species is now lowered to the earliest Eocene, and its known geographic range is now extended northward to the Olympic Peninsula of southwestern Washington (Figures 1, 2).

Since the early paleontologic work by Arnold (1909) in the coal-bearing district of Coalinga in central California, *L. turritum* Gabb, 1868, has been recognized as a component of brackish-marine molluscan assemblages of Eocene rocks of California. Until this present article, however, there has been no attempt to evaluate all of its inferred depositional environments. As will be discussed herein, most of the early Eocene specimens of *L. turritum* were prone to displacement from coastal waters into much deeper waters, whereas middle Eocene specimens are usually found nearly *in situ* in deltaic settings. The species lived for 8.5 million years in humid, tropical to subtropical conditions. The disappearance of *L. turritum* from the fossil record during the early middle Eocene helps confirm data from other sources (paleosols, clay minerals, megafloora, palynomorphs, land-mammals, and land snails) that there was a change in climate at that time to drier conditions.

In this article, the term "shallow-marine" refers to unrestricted, nearshore waters of normal-ocean salinity seaward of beaches or barrier bars. The term "brackish-marine" refers to restricted waters with salinities lower than

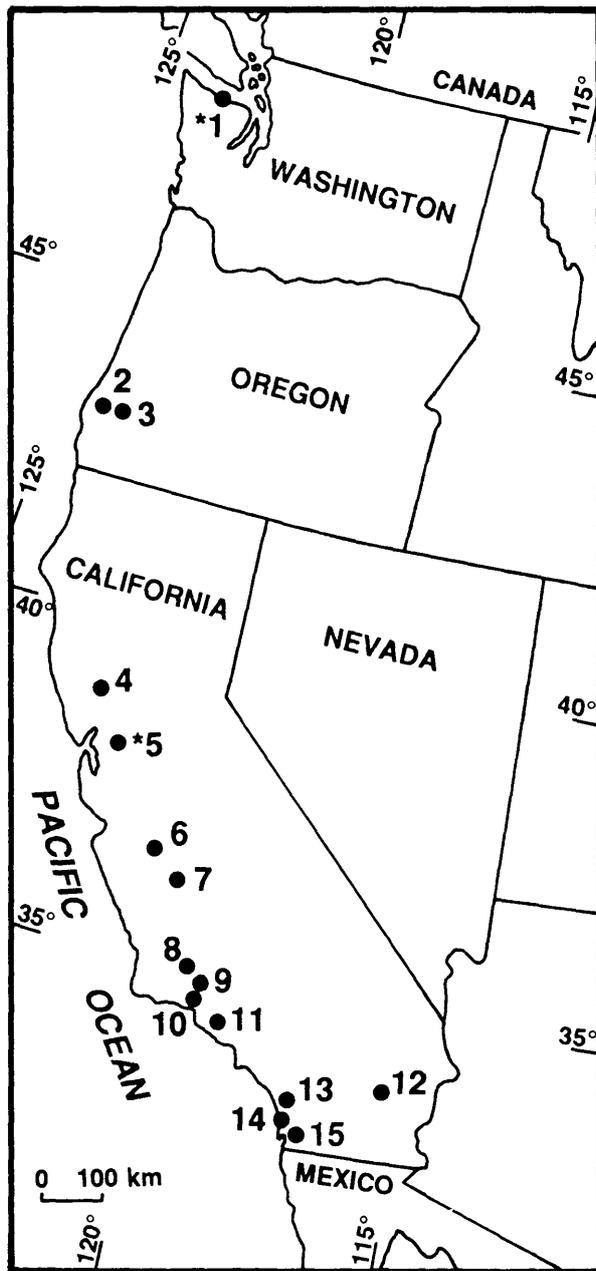


Figure 1

Index map showing geographic locations of *Loxotrema turritum* Gabb, 1868. Locations are numbered from north to south. (1) Crescent Bay. (2) West of Roseburg. (3) Glide. (4) Smith Canyon. (5) Kellogg Creek. (6) Griswold Canyon. (7) Coalmine Canyon. (8) Mouth of Alamo Creek and Beartrap Canyon areas. (9) Pine Mountain. (10) Matilija Hot Springs. (11) Simi Valley. (12) Orocopia Mountains. (13) Vista. (14) Torrey Pines State Reserve and Blacks Canyon areas. (15) Murphy Canyon. (* = New report).

those of normal-ocean waters. Furthermore, the term "brackish-marine" refers to waters landward of beaches or barrier bars but with some connection to the shallow-marine environment.

The following institutional acronyms are used: CAS, California Academy of Sciences, San Francisco; CSUN, California State University, Department of Geological Sciences, Northridge; LACM and LACMIP, Natural History Museum of Los Angeles County, Section of Malacology and Invertebrate Paleontology, Los Angeles, respectively; SDSNH, San Diego Society of Natural History; UCMP, University of California Museum of Paleontology, Berkeley; and UCR, University of California, Riverside.

SYSTEMATIC PALEONTOLOGY

Superorder CAENOGASTROPODA Cox, 1959

Order NEOTAENIOGLOSSA Haller, 1882

Superfamily CERITHIOIDEA Férussac, 1819

Family MELANOPSIDAE Adams & Adams, 1854

Discussion: The family Melanopsidae usually has been regarded as a subfamily of Thiaridae Troschel, 1857. In a cladistic analysis, Houbrick (1988) showed melanopsids to be distinct from thiarids and deserving of full familial status. In his analysis, the Melanopsidae is in a separate branch but relatively close to the branch supporting the Thiaridae.

Subfamily Melanopsinae Adams & Adams, 1854

Discussion: Houbrick (1988, 1991) confusingly assigned subfamily Melanopsinae to the family Thiaridae. Usage of this subfamily name with family Thiaridae, however, is not correct because Melanopsinae, by definition, has to be a subset of family Melanopsidae. It is in the latter sense, that the name Melanopsinae is used in this paper.

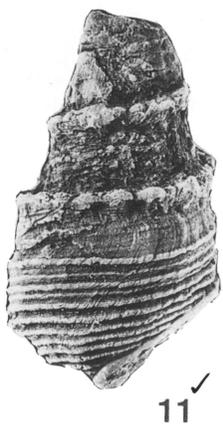
Genus *Loxotrema* Gabb, 1868

Original description: "Shell elongate, turritid, spire high; aperture with a very short canal in front; outer lip retreating above, sinuous below; inner lip heavily encrusted" (Gabb, 1868:147).

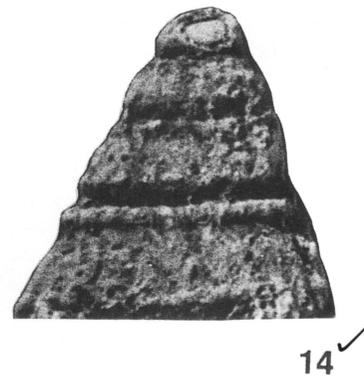
Type species: *Loxotrema turritum* Gabb, 1868, by original designation.

Loxotrema turritum Gabb, 1868
(Figures 3–14)

Loxotrema turrita Gabb, 1868:147, pl. 14, fig. 21; 1869:168, 227, pl. 28, fig. 49. Cooper, 1894:61. Cozzmann, 1904: 103. Arnold, 1909:14, pl. 4, fig. 17. Arnold & Anderson, 1910:71, pl. 26, fig. 17. Arnold & Hannibal, 1913: 572. Dickerson, 1913:285; 1914:115; 1916, 439, 450 (in



UCMP



ent specimens. Aperture obliquely subquadrate, bordered on the inner side by a raised lip, the top retreating upwards, and very obliquely backwards; outer lip thick above and below, very thin in the middle, and with a strongly sinuous margin, most prominent near the anterior end; inner lip thick, its margin somewhat raised above the surface of the body whorl; anterior extremity of aperture not notched, but produced, and slightly channelled" (Gabb, 1869:168).

Supplemental description: Medium in size (up to 45 mm high, estimated), turreted, approximately eight whorls (including protoconch); high-spined, spire about one-half of shell height; body whorl large and cylindrical. Suture in shallow groove, especially on body whorl. Protoconch approximately one whorl, low, smooth, and not well differentiated from teleoconch. Pleural angle approximately 40°. Upper spire whorls convex, remainder of teleoconch with tabulate whorls. Teleoconch sculpture changes from early whorls to later whorls. Uppermost spire whorls with two equal spiral ribs, increasing to three on middle part of spire, with posteriormost rib becoming the strongest. Spiral ribs with numerous, closely spaced small nodes; nodes strongest on posteriormost rib. Interspaces of spiral ribs with two to three very fine spiral threads forming a minute cancellate pattern with the intersecting growth lines. On lower spire and posterior part of body whorl, strength of spiral ribbing quite variable (moderately strong to smooth) and nodes obsolete except on tabulate shoulder, where nodes become very low and broadly spaced on older individuals. On anterior half of body whorl, spiral ribs strong, about eight to 20 in number; interspaces usually with a secondary spiral rib. Aperture obliquely subquadrate. Anterior end with a prominent notch. Siphonal fasciole usually weak, rarely moderately strong. Columella smooth, with a thick callus extending into parietal region and tabulate shoulder area. Posterior end of aperture (where parietal callus meets the tabulate shoulder) with a narrow notch. Outer lip sinuous, with a strong deflection medially. Outer lip projected at its anterior end and thick, thinning considerably toward the strong deflection area. Anteriormost part of outer lip crenulate, both externally and internally. Growth lines prosocline on upper spire, but opisthocline with a strong

sigmoidal curve in region of the strong deflection area of the body whorl. Near suture, growth lines nearly straight to slightly opisthocline. Growth rugae commonly near outer lip on adult body whorl.

Lectotype: ANSP 4228 (designated by Stewart, 1927).

Type locality: "Tejon Group, ten miles west of Griswold's, between San Juan and New Idria" Gabb (1869:168). Vokes (1939:159) referred to topotypes of *L. turritum* from UCMP loc. A-1154, which is in the Domingine Formation, on the west side of Griswold Canyon, San Benito County, central California.

Geographic distribution: Crescent Bay, Olympic Peninsula, southwestern Washington to San Diego area, San Diego County, southern California.

Geologic age: Early Eocene ("Meganos Stage") to lower middle Eocene (lower part of "Tejon Stage").

Stratigraphic distribution: See Table 1.

Unsubstantiated stratigraphic reports: According to Anderson & Hanna (1925:104), Dickerson's (1916) report of *Loxotrema turritum* at the type section of the Tejon Formation in the southernmost part of the San Joaquin Valley, central California, is in error because there is no evidence whatsoever that it does occur there.

Turner (1938:tables 2, 8) reported *L. turritum* from the informal "lower Umpqua group" along the Middle Fork of Coquille River near Remote, southwest of Roseburg in southwestern Oregon. After a careful search, I was unable to find any of these specimens in the UCMP collection, where Turner deposited other specimens that he had collected from Eocene rocks of southwestern Oregon. Although no recent worker has assigned these reportedly *L. turritum*-bearing beds to any currently recognized stratigraphic units, the beds most likely belong to the lower Eocene undifferentiated and informal White Tail Ridge formation that has been recognized in this area by Niem et al. (1992). According to them, this formation in this area is mollusk-bearing and contains delta-front shallow-marine sandstone, as well as rare estuarine coals and mudstone. More work is needed to confirm the presence of *L. turritum* in these rocks.

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Explanation of Figures 3 to 14

Specimens coated with ammonium chloride. Figures 3–14. *Loxotrema turritum* Gabb, 1868. Figures 3–7. Hypotype LACMIP 6449, LACMIP loc. 7206, height 37.3 mm, ×1.8. Figure 3. Apertural view. Figure 4. Right-lateral view. Figure 5. Left-lateral view. Figure 6. Abapertural view. Figure 7. Oblique anterior view. Figure 8. Hypotype LACMIP 6450, LACMIP loc. 7206, right-lateral view, height 34.6 mm, ×1.8. Figures 9–10. Hypotype LACMIP 7162, CSUN loc. 1450, height 28 mm,

×1.9. Figure 9. Left-lateral view. Figure 10. Abapertural view. Figure 11. Hypotype LACMIP 6451, LACMIP loc. 24258, abapertural view, height 20.2 mm, ×2.5. Figure 12. Hypotype UCMP 154003, UCMP loc. A-1550, apertural view, height 21.5 mm, ×2.9. Figures 13, 14. Hypotype LACMIP 6452, LACMIP loc. 7206, apertural view. Figure 13. Height 21.2 mm, ×2.6. Figure 14. Protoconch (some shell missing) and uppermost teleoconch, height 3.5 mm, ×12.

Published reports of *L. turritum* in the Llajas Formation of Simi Valley, Ventura County, southern California are unsubstantiated because of indefinite geologic and geographic information. Kew (1924:29) listed *L. turritum* as one of the mollusks from a locality (UCMP loc. 3311) on the south side of Simi Valley. Using the locality information given by Kew, the locality does not plot in bedrock, rather it plots in the streambed of the modern Simi Arroyo. Information in the UCMP locality records is even less informative, with the locality cited only as Simi Valley. Clark (1921:155) was the original collector of the mollusks from this locality, but he did not include any details as to its location. He listed nearly the same mollusks from this locality that Kew did, but, for some reason, Clark did not include *L. turritum*. I was able to find a specimen of *L. turritum* from UCMP loc. 3311 in the UCMP collection, but the associated mollusks were totally different from those listed by Clark (1921) and Kew (1924) and are ones normally found in the shallow-marine part of the Llajas Formation that crops out on both the north and south sides of Simi Valley. This formation, which was named many years after the work of Clark (1921) and Kew (1924), is an obvious candidate for the stratigraphic position of UCMP loc. 3311. Turner (1938: table 8) even reported, by means of a checklist, that *L. turritum* is present in the "lower Llajas Formation," but he did not provide any other stratigraphic or geographic details. In my monographic study (Squires, 1984) of the megafossils of the Llajas Formation, I found no *L. turritum* anywhere in the formation. I also did a careful search at LACMIP, which has an extensive collection from the Llajas Formation, without finding any specimens of *L. turritum*. I did find several other specimens of *L. turritum* from the Llajas Formation in the collections at UCMP, CAS, and UCR, but the locality data are very indefinite.

Discussion: A total of 297 specimens of *L. turritum* was studied. Most are worn, and the upper spire sculpture usually has been nearly obliterated. The anterior notch and siphonal fasciole are best developed on adult specimens, but even these show variability as to strength of the siphonal fasciole. A weak siphonal fasciole is illustrated in Figure 5, whereas a much stronger one is illustrated in Figures 9 and 10.

The most numerous specimens were found in the Crescent Formation at Crescent Bay, Washington. Nearly all of these are early adults and show very well the sculpture on the upper spire. One of these specimens is illustrated in Figure 12. Some specimens from the upper part of the Matilija Sandstone at Matilija Hot Springs show nodes on the shoulder of the adult body whorl. One of these specimens is illustrated in Figure 11.

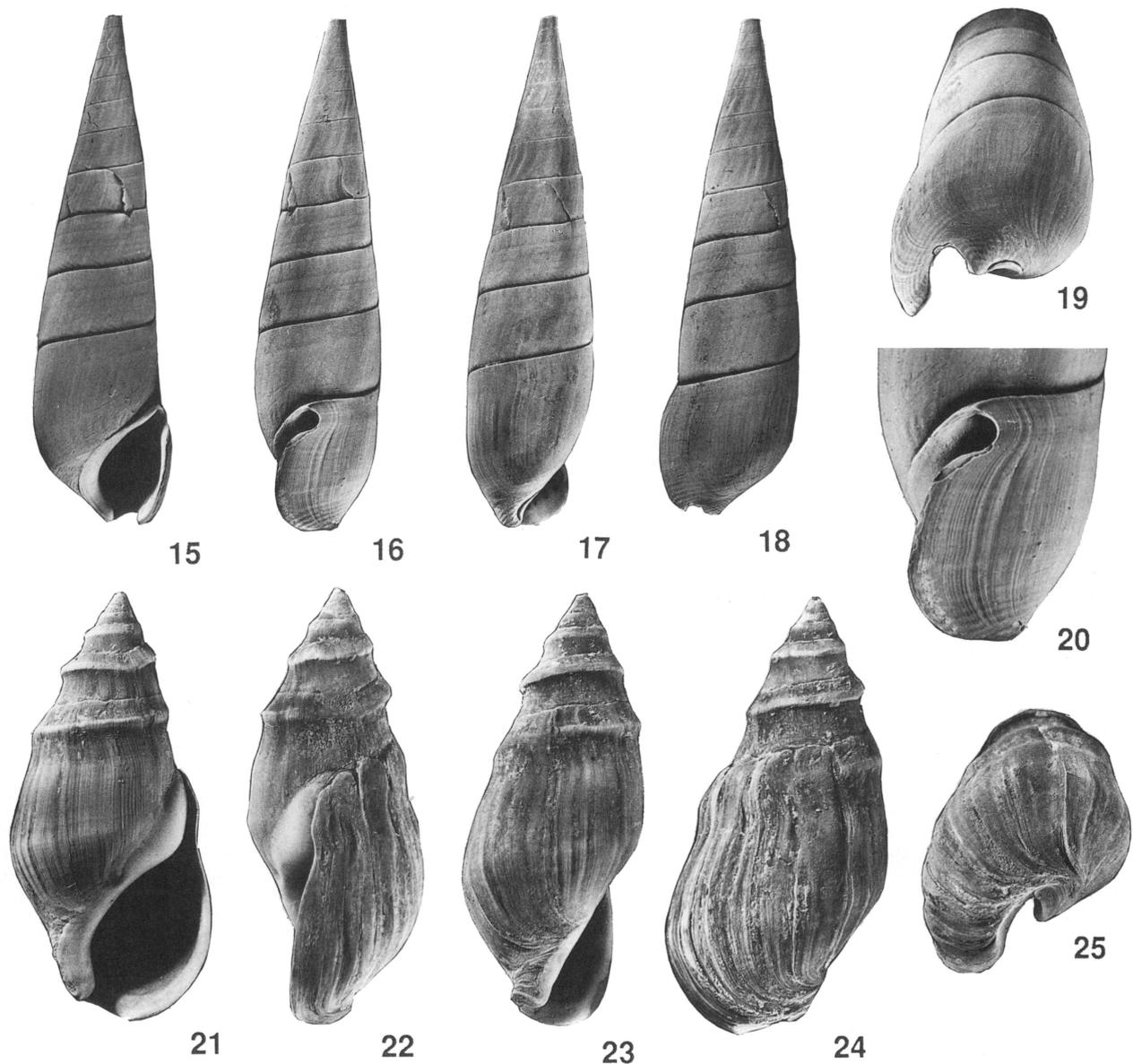
In terms of the apertural notches and outline of the outer lip, *L. turritum* most closely resembles *Faunus ater* Linnaeus, 1758, the type species and only living species

of *Faunus*. Houbrick (1991:figs. 1–18) reported *F. ater* from freshwater to slightly brackish-marine habitats in the Indo-West Pacific. Utilizing LACM specimens (lot number 107993) for comparison, both genera have a subquadrate apertural shape, a well-developed anterior notch, a posterior notch, a projected anterior end of the aperture, a sinuous outer lip, and a siphonal fasciole. A specimen of *F. ater* is illustrated in Figures 15–20. The aperture of *Loxotrema* differs only in minor ways by having shallower anterior and posterior notches, a much narrower posterior notch, usually a weaker siphonal fasciole, and a crenulated anterior end of the outer lip. In terms of the rest of the shell, *Loxotrema* differs by having a much lower spire, tabulate whorls, presence of shell sculpture, no sub-sutural band on the adult body whorl, and deflection of the outer lip-area ophisthoclinal growth lines nearer the suture.

After a detailed anatomical study of *F. ater*, Houbrick (1991) assigned *Faunus* to subfamily Melanopsinae and reported that *F. ater* has certain unusual anatomical features that unite *Faunus* to the melanopsid *Melanopsis* and to the thiarid *Melanatria* Bowdich, 1822. Houbrick (1991) also discussed how the classification of *Faunus* is still very provisional and that much work is needed to clarify its exact phylogenetic relationship with the thiarid group, a large and poorly defined family of freshwater prosobranchs in need of major revision.

Loxotrema turritum closely resembles the living species *Melanopsis (Lyrcaea) dufouri* Férussac, 1823, the type species of *Lyrcaea*. *Melanopsis (L.) dufouri* was illustrated by Wenz (1939:691, fig. 1987), who reported it from Valencia, Spain. Subgenus *Lyrcaea* is generally smoothish, ranges from Eocene to Recent, and its fossil record is in Europe, North Africa, and Asia. Today it is confined to the Mediterranean region (Wenz, 1939). Comparison with LACM specimens (lot number 108173) of *M. (L.) dufouri*, from a floodplain-river system near Seville, Spain, revealed that *Loxotrema turritum* differs from this species by having a higher spire, shorter body whorl, spiral ribbing on the whorls rather than just a swollen spiral rib at the whorl shoulder, an oblique posterior notch rather than a vertical one, usually a much weaker siphonal fasciole, and a more sigmoidal growth line on the body whorl. A specimen of *M. (L.) dufouri* is illustrated in Figures 21–25.

Loxotrema turritum is also somewhat similar to *Cerithium? macarum* Olsson (1931:183–184, pl. 28, fig. 3) in terms of general shape, upper spire ornamentation, and growth-line shape on the body whorl. *Cerithium? macarum*, which has been found in the Oligocene Mancora Formation of Peru, is known from only a single specimen, and it lacks the aperture and the tip of the spire. *Loxotrema turritum* differs from this species by having a longer body whorl, much shorter spire, more inflated body whorl, more prominent spiral ribs on body whorl, more tabulate and nodose shoulder on the whorls, and no in-



Explanation of Figures 15-25

Specimens coated with ammonium chloride.

Figures 15-20. *Faunus ater* Linnaeus, 1758, hypotype LACM 107993, Recent, Sri Lanka (Ceylon), height 63 mm, $\times 1.2$ Figure 15. Apertural view. Figure 16. Right-lateral view. Figure 17. Left-lateral view. Figure 18. Abapertural view. Figure 19.

Oblique anterior view. Figure 20. Enlarged right-lateral view of body whorl. Figures 21-25. *Melanopsis (Lyrcaea) dufouri* Férussac, 1823, hypotype LACM 108173, Recent, Sevilla, Spain, height 25.4 mm, $\times 2.4$. Figure 21. Apertural view. Figure 22. Right-lateral view. Figure 23. Left-lateral view. Figure 24. Abapertural view. Figure 25. Oblique anterior view.

dication of varices. Until better material is found for Olson's species, its generic assignment is open to question.

Loxotrema turritum generally resembles the living species *Aylacostoma glabrum* Spix, 1827 (in Spix & Wagner, 1827), which is the type species of *Aylacostoma*. *Aylacostoma glabrum* was recently described and illustrated by Nuttall (1990:259, 261, figs. 286-291), who reported

it from a freshwater habitat in eastern Brazil. This genus belongs to family Thiariidae and subfamily Hemisininae Thiele, 1928. The only other known species of this genus is *Aylacostoma* sp., which is based on poorly preserved specimens of Miocene age from Ecuador (Nuttall, 1990). *Aylacostoma glabrum* shows considerable variation in morphology. It can be smooth or have rather strong sculp-

ture, and the body whorl can be almost straight-sided or strongly shouldered with a marked ramp. All of these variants are well illustrated by Nuttall (1990). *Loxotrema turritum* resembles only those specimens of *A. glabrum* that are smoothish and strongly shouldered (see Nuttall, 1990:figs. 286–287) and differs significantly from them by having a posterior notch in the aperture, a protruding (hoodlike) anterior portion of the outer lip rather than a slight concavity there, a weak siphonal fasciole, a sigmoidal growth line rather than a slightly sinuate one, shorter spire, tabulate spire whorls, beaded upper spire whorls, and a projecting and much thicker callus along the inner lip. In addition, *L. turritum* does not have a ramp associated with its strongly tabulate body whorl shoulder. In spite of the many differences between these two taxa, their overall similarity does suggest a case of convergence.

Loxotrema turritum is only the second melanopsid recognized in the fossil record of the Pacific slope of North America. The other one is *Boggsia tenuis* (Gabb, 1864), known from the Upper Cretaceous (Campanian Stage) strata in northern California (Squires & Saul, 1997).

The name *Loxotrema* is a combination of *loxos* (Greek, slanting or crosswise) and the neuter noun *trema* (Greek, hole). Although early workers used the name “*turrita*,” Fischer (1884) was correct in using the name “*turritum*” because *turritus* (Latin, with towers or castellated) is an adjective and its ending has to agree in gender with the genus.

STRATIGRAPHIC DISTRIBUTION AND DEPOSITIONAL ENVIRONMENTS

Introduction

Loxotrema turritum is known from numerous areas in California, two areas in Oregon, and one area in Washington (Figure 1). Its geologic range for each of these states is depicted in Figure 2. The formations in which it is found, as well as the associated inferred depositional environments, are given in Table 1.

“Meganos Stage”

The only known “Meganos Stage” record of *L. turritum* is new information. It is also the earliest record of this species, which was reported formerly by various workers (Table 1) to be no earlier than the “Capay Stage.” The “Meganos Stage” record is based on a single worn specimen from a sandstone (UCMP loc. 3586) in the Kellogg Creek area of Contra Costa County in northern California. This sandstone was referred to as “division D of the Meganos Formation” by Clark & Woodford (1927), but modern workers use the name “Margaret Hamilton Sand” (Edmondson, 1984). Division D of the Meganos Formation is correlative with the middle of the CP9 Zone of the standard calcareous nannoplankton zo-

nation (Almgren et al., 1988). This part of the CP9 Zone is correlative with the “Meganos Stage” (Squires, 1988a). Almgren (1978) reported the Margaret Hamilton Sand to contain benthic foraminifera indicative of a probable mid-neritic (shallow marine) environment of deposition. The mollusks found associated with *L. turritum* at UCMP loc. 3586 (Clark & Woodford, 1927:82–84) also indicate a shallow-marine environment. The broken and worn condition of the *L. turritum* specimen indicates that it was probably transported to the site.

“Capay Stage”

Only a single CSUN collection specimen was found in the “Capay Stage” Maniobra Formation of the Orocopia Mountains of Riverside County in southern California. This specimen, which is poorly preserved and worn, was tentatively identified (Squires, 1991b:pl. 1, fig. 16, table 1) as *L. turritum*. I now consider it to be *L. turritum*. This specimen is part of a relatively diverse and mostly shallow-marine megafossil assemblage that was interpreted as having lived in nearshore waters adjacent to a submarine canyon and was transported basinward into the bathyal depths of the submarine canyon (Advocate et al., 1988; Squires, 1991b).

Merriam & Turner (1937:table 2) reported *L. turritum* as part of a moderately diverse and mostly shallow-marine megafossil assemblage from the Capay Formation at the type section of the formation as Smith Canyon, Yolo County, northern California. I examined the UCMP collection specimens and found them to be poorly preserved. Redwine (1984) reported that the lower Eocene Capay Formation represents displaced material derived mostly from nearshore depths and deposited as turbidites in the lower part of the Princeton Submarine Valley system, whose length was approximately 265 km. These *L. turritum* specimens, therefore, probably underwent considerable postmortem transport.

The “Capay Stage” specimens of *L. turritum* from Crescent Bay, Washington (UCMP locs. A-1547, A-1550) represent a new occurrence and extend, a distance of 580 km, this species’ northernmost record, which was previously reported to be in southwestern Oregon (Turner, 1938). These Washington specimens differ from other “Capay Stage” specimens by having lived in coastal waters on the flank of a basalt volcano. These abundant and well-preserved UCMP collection specimens, all about 22 mm high and showing the delicate upper spire sculpture, were found in sedimentary interbeds in basalt flows of the Crescent Formation on the west side of Crescent Bay, Clallam County, Olympic Peninsula, southwestern Washington. Duncan (1982) proposed that this Crescent Formation basalt formed oceanic seamounts that became accreted, by means of subduction-zone tectonics, to the margin of the North American continent. More recently, Babcock et al. (1992) proposed that the basalt formed

Table 1

Formations containing *Loxotrema turritum* and their inferred depositional environments. Stages listed youngest to oldest, in descending order. [CA = California, OR = Oregon, WA = Washington, * = New occurrence].

| Formation; location; literature sources | Inferred depositional environment; literature sources |
|---|--|
| "TEJON STAGE": | |
| Matilija Sandstone, Pine Mtn., Ventura Co., CA (Givens, 1974) | Mixed brackish-marine bays or lagoons & shallow marine at the seaward margin of a delta complex (Givens, 1974) |
| Matilija Sandstone, mouth of Alamo Creek, Ventura Co., CA (Givens, 1974) | Brackish-marine bays or lagoons on a delta complex (Givens, 1974) |
| Juncal Formation (sandstone facies), Pine Mtn., Ventura Co., CA (Givens, 1974) | Mixed brackish-marine bays or lagoons & shallow marine (beach & bar) at the seaward margin of a delta complex (Givens, 1974) |
| Matilija Sandstone, Beartrap Creek, Ventura Co., CA (Squires, 1991a) | Mixed brackish marine & nearshore marine (Squires, 1991a) |
| "TRANSITION STAGE": | |
| Matilija Sandstone, Matilija Hot Springs, Ventura Co., CA (Squires, 1991a) | Brackish-marine lagoon or bay in close association with beach-bar-barrier complexes (Link, 1975; Link & Welton, 1982; Squires, 1991a) |
| Juncal Formation (siltstone facies), NE of Pine Mtn., Ventura Co., CA (Givens, 1974) | Interdistributary bays or lagoons or prodelta at the seaward margin of a delta complex (Givens, 1974) |
| Scripps Formation, Murphy Canyon, San Diego Co., CA (Squires & Demere, 1991) | Nearshore shallow-marine with some transported brackish-marine lagoonal mollusks (Squires & Demere, 1991) |
| "DOMENGINE STAGE": | |
| *Ardath Shale, Blacks Canyon, San Diego Co., CA | Bathyal (600 to 1500 m depth) submarine-fan channel fill with reworked shallow-marine fossils (Lohmar et al., 1979; May & Warme, 1991) |
| Delmar Formation, Torrey Pines State Reserve, San Diego Co., CA (Hanna, 1927; Givens & Kennedy, 1979) | Marginal-marine oyster bioherms in a bay, estuary, or lagoon (Hanna, 1926; Lohmar et al., 1979; Warme, 1991; May & Warme, 1991) |
| Santiago Formation, Vista, San Diego Co., CA (Givens & Kennedy, 1976) | Marine or brackish marine, perhaps lagoon or estuary (Givens & Kennedy, 1976) |
| Domengine Formation, Vallecitos syncline, San Benito Co., CA (Vokes, 1939; Schulein, 1993) | Brackish-marine lagoon on a deltaic complex (Schulein, 1993) |
| Domengine Formation, Coalmine Canyon, Fresno Co., CA (Arnold, 1909; Arnold & Anderson, 1910; Vokes, 1939) | Swampy intertidal distributary bay on a delta complex (Roush, 1986) |
| "CAPAY STAGE" | |
| White Tail Ridge formation, Glide, Douglas Co., OR (Turner, 1938) | Mixed fluvial & shallow marine on a delta complex (Niem et al., 1992) |
| *Crescent Formation, Crescent Bay, Clallam Co., WA | Rift-zone? volcanic island in marine waters (Babcock et al., 1992) |
| Maniobra Formation, Orocopia Mtns., Riverside Co., CA (Squires, 1991b) | Bathyal submarine-canyon fill, very near a coastline (Advocate et al., 1988; Squires, 1991b). |
| Capay Formation, Smith Canyon, Yolo Co., CA (Merriam & Turner, 1937) | Bathyal (760 to 1830 m depth) submarine-valley fill (Redwine, 1984) |
| "MEGANOS STAGE" | |
| *Margaret Hamilton Sand, Kellogg Creek, Contra Costa Co., CA | Probable mid-neritic (shallow marine) (Almgren, 1978) |

volcanic islands within a rift zone along the margin of the continent, and this tectonic setting seems much more likely for *L. turritum* than one associated with oceanic seamounts. At UCMP loc. A-1547, *L. turritum* was found associated with a diverse shallow-marine, mega-invertebrate assemblage consisting of many species of mollusks and a species of colonial coral. Many of these same species of mollusks were reported by Arnold & Hannibal (1913:572) from the Crescent Formation near Tongue Point on the east side of Crescent Bay. At UCMP loc. A-

1550, *L. turritum* was found associated with shallow-marine mollusks and some specimens of the gastropod *Potamides (Potamides?) carbonicola* Cooper, 1894. This potamidid has been reported by many workers (e.g., Arnold, 1909) as diagnostic of brackish-marine environments. The presence of it in the Crescent Formation is new information. Elsewhere in southwestern Washington, the upper part of the Crescent Formation has yielded mollusks and other megafossils that lived on the hard substrate formed where extrusion of basalt caused shoaling

of marine waters. The megafaunas were subject to storm waves and were transported down steep slopes into shallow, subtidal depths where other mollusks lived (Squires et al., 1992; Squires & Goedert, 1994a, b, 1995, 1996). In all these previously studied areas, however, *L. turritum* has not been found, but at one locality in the Crescent Formation at Larch Mountain, Black Hills near Olympia, Squires & Goedert (1994a) reported the presence of the ellobiid *Ovatella* (*Myosotella*), a pulmonate (air-breathing) gastropod indicative of salt marshes and upper shores or estuaries. Evidently, the early Eocene volcanic island in the Crescent Bay region was associated with localized brackish-marine environments. The uniform size of the *L. turritum* specimens indicates sorting associated with post-mortem transport, but the presence of delicate upper spire sculpture on these specimens indicates that the distance of transport was not great. Detailed paleo-environmental studies of the Crescent Formation in the Crescent Bay area are much needed.

The taphonomy of the specimens of *L. turritum* from the Maniobra, Capay, and Crescent formations is similar to that reported (Givens, 1994; Squires & Advocate, 1986; Squires, 1997) for some other early Eocene gastropods that lived in coastal waters along the tectonically active coast of California. Like *L. turritum*, they were subject to transport into deeper waters via turbidity currents.

Turner (1938) reported specimens of *L. turritum* in the Glide area of southwestern Oregon. The specimens are from the informal White Tail Ridge formation (A. Niem, personal communication, 1996), which is correlative to the upper Umpqua formation or the Lookingglass Formation, both of previous usage (Niem et al., 1992). The White Tail Ridge formation is assignable to the lower Eocene calcareous nannofossil CP11 Zone, which ranges from the upper part of the "Capay Stage" to the lower part of the "Domengine Stage" (Squires, 1988a). Givens & Kennedy (1976) believed that the rock unit at Glide might possibly be assignable to the "Domengine Stage," but the presence of *Turritella andersoni* Dickerson, 1916, a species diagnostic of the "Capay Stage" (Squires, 1988b), indicates that the rock unit is assignable to the "Capay Stage." It is likely that the Glide specimens are in rocks correlative to near the boundary between the "Capay Stage" and the "Domengine Stage." Although the White Tail Ridge formation consists of deltaic (mixed fluvial and shallow-marine) deposits (Niem et al., 1992), the actual beds containing the specimens of *L. turritum* have not been incorporated by any recent worker into a detailed depositional-model context. Several years ago, before I began this present investigation, I collected specimens of *L. turritum* from this formation in the Glide area at UCMF locs. A-661 and A-662. The specimens are in sandy lenses of transported fossils, and the lenses are about 15 to 20 m in lateral extent. The richest lens is at locality A-661, which is about 5 m stratigraphically be-

low the lens at locality A-662. At locality A-661, there are abundant specimens of *L. turritum*, ranging in height from 17 to 40 mm (estimated). Many of them are nearly complete and are missing only the protoconch, the anterior end of the aperture, and the outer lip. The upper spire sculpture has been somewhat abraded, and although the specimens have undergone some postmortem transport they were not transported very far. Overall, the shells at this locality show better preservation than at any other locality where *L. turritum* has been found. There are also a few specimens of *Potamides* (*P.?*) *carbonicola* present at locality A-661.

"Domengine Stage"

Arnold (1909) and Arnold & Anderson (1910) reported *L. turritum* from a section of middle Eocene rocks containing lignite and gypsiferous sandstone at Coalmine Canyon about 7 km northwest of Coalinga, central California, and they interpreted that these rocks were brackish marine. These rocks are now referred to as the Domengine Formation (Vokes, 1939:20). Roush (1986:81, figs. 5B, 25) studied the details of the depositional environment of the Domengine Formation at Coalmine Canyon, and although she found no *L. turritum*, she interpreted that the beds accumulated in an interdistributary bay on a river-dominated delta associated with a low-energy coastline where swamps were present.

Vokes (1939) reported *L. turritum* from the Domengine Formation in the Vallecitos syncline area between New Idria and Panoche, about 50 km north of Coalinga. In addition, he confirmed the presence of this species in the Domengine Formation at Coalmine Canyon. Vokes (1939:159) reported, furthermore, that *L. turritum* is a brackish-marine species and is always associated with *Acutostrea idriaensis idriaensis* (Gabb, 1869) and *Potamides* (*P.?*) *carbonicola*. He did not make it clear if he was referring to only the Vallecitos syncline area or to everywhere *L. turritum* is present. *Loxotrema turritum* is not always associated with these two species. Schulein (1993) studied the details of the depositional environment of the Domengine Formation in the Vallecitos syncline area. In the Griswold Canyon area in the central part of this syncline, he found *L. turritum*, usually associated with *P. (P.?) carbonicola* and *A. idriaensis idriaensis*, in lenses interbedded with carbonaceous claystone and siltstone. He interpreted the formation in this particular area as having been deposited on a deltaic complex and that these species represent nearly *in situ* brackish-marine lagoonal assemblages, or that they had undergone slight postmortem transport and accumulated at the seaward edge of a salt marsh.

Givens & Kennedy (1976) reported *L. turritum* from a small molluscan assemblage in middle Eocene ("Domengine Stage") strata near Vista in northern San Diego County, southern California. Although none of the spec-

imens of this species is complete, they show good preservation and their depositional environment was interpreted (Givens & Kennedy, 1976) as having been "a low-energy, very shallow (0–30 m) marine or brackish-water environment, perhaps in a lagoon or estuary." These rocks are now assigned to the Santiago Formation (Eisenberg & Abbott, 1991).

Hanna (1926) reported *L. turritum* from the Delmar Formation near San Diego, and he interpreted the formation to be a brackish-marine deposit. Many sedimentological studies in recent years (e.g., Kennedy & Moore, 1971; Lohmar et al., 1979; Warme, 1991; May & Warme, 1991) have supported the interpretation that the Delmar Formation was deposited in a stream-mouth lagoonal setting.

The presence of rare reworked specimens of *L. turritum* in the Ardath Shale at Blacks Canyon, San Diego County, southern California, represents the only post-"Capay Stage" record of this species in deep-marine rocks. This occurrence is new information. The specimens, which are from the upper 4 m of the Ardath Shale at UCR loc. 4930, have their apertures filled with clean, medium-grained sand matrix that is distinctly different from the surrounding siltstone, thereby indicating that the shells were transported prior to burial. The Ardath Shale consists of canyon fill deposited at depths between 600 and 1500 m. The submarine canyon incised into older shallow-water deposits of the Delmar Formation and other formations (Lohmar et al., 1979; May & Warme, 1991), and the Delmar Formation was most likely the source for the specimens of *L. turritum*.

"Transition Stage"

Roth (1988) and Squires & Demere (1991) reported *L. turritum* from SDSNH loc. 3278 in the Friars Formation at Murphy Canyon in the San Diego area. Walsh et al. (1996), however, reassigned the rocks at this locality to the laterally interfingering and subjacent upper part of the Scripps Formation. The *L. turritum* at this locality represents part of a transported and rare, but distinct, brackish-marine element of an otherwise moderately diverse nearshore, shallow-marine molluscan assemblage (Roth, 1988; Squires & Demere, 1991).

Givens (1974:table 1) reported *L. turritum*, along with *Potamides* (*P.?*) *carbonicola* and *Acutostrea idriaensis idriaensis*, at a single locality (UCR loc. 4696) in the *Ectinochilus supraplicatus* megafaunal biozone in the siltstone facies of the Juncal Formation about 2.5 km northeast of Pine Mountain, Ventura County, southern California. He also interpreted that the siltstone facies might have been deposited in interdistributary bays or lagoons or in the prodelta environment of the seaward edge of the deltaic complex.

The middle Eocene upper part of the Matilija Sandstone at Matilija Hot Springs in Ventura County, southern

California contains numerous specimens of *L. turritum* within a 50 m-thick section of alternating sandstone and finer grained intervals consisting of complexly interbedded mudstone, fossiliferous mudstone, siltstone, and, in some cases, gypsum and limestone. Link (1975) and Link & Welton (1982) reported the section represents a restricted-coastal (paralic) environment, with three main subenvironments: beach-bar-channel complexes [= sandstone], lagoon or bay [= mudstone, fossiliferous mudstone, and siltstone], and coastal sabkha [= gypsum, limestone, mudcracks, and localized "red beds"]. Based on my own fieldwork, which is being incorporated into a detailed report of the molluscan fauna of these restricted-coastal rocks (Squires, in preparation), I found that *L. turritum* is present in several thin, silty mudstone beds immediately overlain by unfossiliferous mudstone or siltstone. Common associates are the gastropod *Potamides* (*Potamidopsis*) *californica* Squires, 1991a, the oyster *Acutostrea idriaensis idriaensis*, and corbiculid, tellinid, and venerid bivalves. The specimens of *L. turritum* and *P. (P.) californica* range in size from early juveniles to adults, show delicate sculpture, are mostly complete, and are randomly oriented. Many of the bivalve specimens are closed-valved. The distance of postmortem transport of any of these mollusks has been small, and the specimens have not been moved out of their original habitat. They represent nearly *in situ* brackish-marine individuals that lived in restricted-coastal waters. Some of the fossiliferous mudstones in this section contain lenses of gypsum and/or limestone. In comparison with the other fossiliferous mudstones, these mudstones directly associated with evaporites have a much lower taxonomic diversity of mollusks. Although *Potamides* (*Potamidopsis*) *californica* persists as a common faunal component in these mudstones associated with evaporites, *L. turritum* is never present, and its absence indicates that it did not tolerate evaporitic conditions.

"Tejon Stage"

Jestes (1963) and Squires (1991a) reported a storm-derived mixture of nearshore-marine and brackish-marine mollusks, including *L. turritum*, in the Matilija Sandstone in the vicinity of Beartrap Creek, just east of the mouth of Alamo Creek, Ventura County, southern California. Givens (1974) assigned the rocks in this part of the Matilija Sandstone to the "Tejon Stage."

Givens (1974:table 1) reported *L. turritum* from the *Ectinochilus canalifer* megafaunal biozone in the sandstone facies of the Juncal Formation just north of Pine Mountain, Ventura County, southern California. Some mollusks in this facies are indicative of the shallow-marine environment, possibly at the seaward margin of a delta complex, whereas others (oyster banks and *Potamides* (*P.?*) *carbonicola*) are indicative of brackish-water bays or lagoons (Givens, 1974).

Givens (1974:table 1) also reported *L. turritum* from the *Ectinochilus canalifer* biozone in the lower part of the Matilija Sandstone at the mouth of Alamo Creek, Ventura County, southern California. Associated mollusks (e.g., *Potamides* (*P.*?) *carbonicola* and *Acutostrea idriaensis idriaensis*) indicate that these rocks were probably deposited in brackish-water bays or lagoons (Givens, 1974).

Givens (1974:table 1), furthermore, reported a mixture of shallow-marine and brackish-marine mollusks, including *L. turritum*, in the *Ectinochilus canalifer* biozone in the Matilija Sandstone just east of Pine Mountain, Ventura County, southern California, and he interpreted the depositional environment of these mollusks to have been probably adjacent to a delta complex.

PALEOCLIMATE

Introduction

Inferred paleoclimatic conditions for the geologic range of *L. turritum* are summarized in Figure 2. Eocene rocks in San Diego County, southern California, are particularly useful for paleoclimate studies because of the complex intertonguing relationships between shallow-marine and nonmarine formations. These stratigraphic relationships span nearly the entire Eocene, and many types of geologic studies have been done on these rocks.

"Meganos Stage" and "Capay Stage"

Loxotrema turritum was most widespread (from Washington to southern California) during the time of the "Meganos Stage" and the "Capay Stage." This early Eocene time was the warmest interval of the Cenozoic, and tropical to subtropical conditions were widespread (Haq, 1981). On the west coast during this time, tropical and hot-humid conditions prevailed in coastal-lowland areas, as revealed by studies of a lateritic paleosol and of megafossil (Figure 2). The paleosol study was done in the San Diego area, southern California, and in northwestern Baja California, Mexico (Peterson & Abbott, 1979). The megafossil study was done on the lower Eocene part of the Puget Group of southwestern Washington (Wolfe, 1968; 1994).

"Domengine Stage"

The "Domengine Stage" record of *L. turritum* is known only from California. From the middle part of this stage (lowermost middle Eocene) through the end of the geologic range of this species in the lower part of the "Tejon Stage" (lower middle Eocene), *L. turritum* is known only from southern California. During this same interval, tropical to subtropical conditions were prevalent in coastal-lowland areas, as revealed by studies of clay mineralogy, megafossil, palynomorphs, and land snails (Figure 2). The clay mineralogy study was done on the Domengine Formation in northern California (Todd,

1968; Todd & Monroe, 1968), and the megafossil studies were done on the Torrey Sandstone in the San Diego area (Myers, 1991). This latter formation has been reported by many workers (e.g., May & Warne, 1991) as interdigitating laterally with both the marine Ardath Shale and the brackish-marine Delmar Formation. Palynomorph studies were done on the Ardath Shale (Lowe, 1974; quoted in Lillegraven, 1979), on the Delmar Formation (Elsik & Boyer, 1977), and on the Domengine Formation in the Vallecitos syncline area in northern California (Schulein, 1993). A land snail was studied from the Santiago Formation at Oceanside in northern San Diego County (Roth, 1991).

"Transition Stage"

The Scripps Formation record of *L. turritum* at Murphy Canyon (SDSNH loc. 3278) in the San Diego area is also associated with land snails. A study of camaenid land snails from the upper part of this formation indicated "forested land and a tropical climate with ample summer rainfall," and the land snails might have been living in a humid forest fringing a coastal lagoon (Roth, 1988). A single specimen of a transported helicid land snail from elsewhere in the Scripps Formation could indicate tropical conditions, but paleoclimate inferences based on helicids are somewhat inconclusive because modern members of this family range into xeric (dry) habitats (Roth & Pearce, 1988).

Lower Part of the "Tejon Stage"

In the San Diego area, the Scripps Formation laterally interfingers with and is partly subjacent to the chiefly nonmarine Friars Formation. Just upsection from the Friars Formation is the marine to nonmarine Mission Valley Formation. Neither of these two formations contains specimens of *L. turritum*, but both (especially the Mission Valley Formation) record a climatic change to less humid conditions (Peterson & Abbott, 1979). The Mission Valley Formation is correlative in time to just after the disappearance of *L. turritum* from the rock record. Frederickson (1991b) assigned this formation to the calcareous nannoplankton Subzone CP13c, but Walsh et al. (1996) suggested that it might be assignable to the slightly younger Subzone CP14a (equivalent to the lower part of the "Tejon Stage"). Caliche horizons, immature clay-mineral suites, and apparent salt crystallization from the Friars and Mission Valley formations have led to the conclusion that the paleoclimate during the deposition of these rock units was distinctly seasonal and arid (Peterson & Abbott, 1979). A study of over 100 species of land vertebrates from these same formations have led to the conclusion that the paleoclimate was seasonal and dry to moist sub-humid (Novacek & Lillegraven, 1979). Frederickson (1991a) reported that the angiosperm-pollen flora from near the base of the Mission Valley Formation indicates

that the climate was seasonal and no dryer than moist subhumid.

The synchronism between the disappearance of *Loxotrema turritum* and the change of climate from subtropical/tropical to seasonal semiarid strongly suggests that the extinction of this species was caused by climatic change. The species was adapted for humid, tropical conditions as evidenced by its widespread dispersal during the early Eocene. It is important to mention that the environment of *Faunus ater*, which is the closest living relative of *Loxotrema turritum*, is also confined to fully tropical conditions. *Faunus ater* is found today in the mouths and coastal reaches of freshwater rivers and streams, where there is some brackish influence, between 20°N and 20°S of the equator in southeast Asia, Sumatra, Java, Moluccas, Thailand, Sri Lanka (Ceylon), China, Philippines, New Guinea, Solomon Islands, and New Hebrides (Houbick, 1991).

The presence of *L. turritum* in nearly *in situ* conditions in the upper part of the Matilija Sandstone at Matilija Hot Springs is especially revealing. As discussed earlier, it is present in fossiliferous mudstones not directly associated with evaporites, but it is always absent in fossiliferous mudstones containing lenses of evaporites. Although *Loxotrema turritum* was rather hardy because it lived in the brackish-marine environment, it could not tolerate arid conditions, and it is very likely that when the climate became too dry during the early middle Eocene the species went extinct.

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LITERATURE CITED

- ADVOCATE, D. M., M. H. LINK & R. L. SQUIRES. 1988. Anatomy and history of an Eocene submarine canyon: the Maniobra Formation, southern California. Pp. 45–58 in M. V. Filewicz & R. L. Squires (eds.), *Paleogene Stratigraphy, West Coast of North America*. Pacific Section, Society of Economic Paleontologists and Mineralogists, Volume 58: Los Angeles, California.
- ALMGREN, A. A. 1978. Timing of Tertiary submarine canyons and marine cycles of deposition in the southern Sacramento Valley, California. Pp. 276–291 in D. J. Stanley & G. Kelling (eds.), *Sedimentation in Submarine Canyons, Fans and Trenches*. Dowden, Hutchinson & Ross: Stroudsburg, Pennsylvania.
- ALMGREN, A. A., M. V. FILEWICZ & H. L. HEITMAN. 1988. Lower Tertiary foraminiferal and calcareous nannofossil zonation of California: An overview and recommendation. Pp. 83–105 in M. V. Filewicz & R. L. Squires (eds.), *Paleogene Stratigraphy, West Coast of North America*. Pacific Section, Society of Economic Paleontologists and Sedimentologists. Vol. 58: Los Angeles, California.
- ANDERSON, F. M. & G. D. HANNA. 1925. Fauna and stratigraphic relations of the Tejon Eocene at the type locality in Kern County, California. *Occasional Papers of the California Academy of Sciences* 9:1–249, pls. 1–16.
- ARNOLD, R. 1909. Paleontology of the Coalinga district, Fresno and Kings counties, California. U.S. Geological Survey Bulletin 396:1–173, pls. 1–30.
- ARNOLD, R. & R. ANDERSON. 1910. Geology and oil resources of the Coalinga district, California. U.S. Geological Survey Bulletin 398:1–354, pls. 1–52.
- ARNOLD, R. & H. HANNIBAL. 1913. The marine Tertiary stratigraphy of the north Pacific coast of America. *Proceedings of the American Philosophical Society* 52(212):559–605.
- BABCOCK, R. S., R. F. BURMESTER, D. C. ENGBRETSON & A. WARNOCK. 1992. A rifted margin origin for the Crescent basalts and related rocks in the northern Coast Range volcanic province, Washington and British Columbia. *Journal of Geophysical Research* 97(B5):6799–6821.
- BALDWIN, E. M. 1959. *Geology of Oregon*. University of Oregon Cooperative Book Store: Eugene, Oregon. 130 pp., 35 pls.
- BERGGREN, W. A., D. V. KENT, C. C. SWISHER, III & M.-P. AUBRY. 1995. A revised Cenozoic geochronology and chronostratigraphy. Pp. 129–212 in W. A. Berggren, D. V. Kent, M.-P. Aubry & J. Hardenbol (eds.), *Geochronology, Time Scales, and Global Stratigraphic Correlation*. SEPM (Society for Sedimentary Geology) Special Publication 54.
- CLARK, B. L. 1921. The stratigraphic and faunal relationships of the Meganos Group, middle Eocene of California. *Journal of Geology* 29:125–165.
- CLARK, B. L. 1926. The Domengine horizon, middle Eocene of California. University of California Publications, Bulletin of the Department of Geological Sciences 16(5):99–118.
- CLARK, B. L. 1929. *Stratigraphy and Faunal Horizons of the Coast Ranges of California, with Illustrations of Index Fossils of Tertiary Horizons*. Privately published. 30 pp., 50 pls.
- CLARK, B. L. & A. O. WOODFORD. 1927. The geology and paleontology of the type section of the Meganos Formation (lower middle Eocene) of California. University of California Publications, Bulletin of the Department of Geological Sciences 17:63–142, pls. 14–23.
- COOPER, J. G. 1894. Catalogue of California fossils. *California State Mining Bureau Bulletin* 4:1–65, pls. 1–6.
- COSSMAN, M. 1904. *Essais de Paléoconchologie Comparée*. Sixième Livraison. 151 pp., 9 pls.
- DICKERSON, R. E. 1913. Fauna of the Eocene at Marysville Buttes, California. University of California Publications, Bulletin of the Department of Geology 7(12):257–298, pls. 11–14.
- DICKERSON, R. E. 1914. The fauna of the *Siphonalia sutterensis* Zone in the Roseburg Quadrangle, Oregon. *Proceedings of the California Academy of Sciences*, 4th series, 4:113–128, pls. 11–12.
- DICKERSON, R. E. 1916. Stratigraphy and fauna of the Tejon Eocene of California. University of California Publications, Bulletin of the Department of Geology 9(17):363–524, pls. 36–46.
- DUNCAN, R. A. 1982. A captured island chain in the Coast Range of Oregon and Washington. *Journal of Geophysical Research* 7:10,827–10,837.
- EDMONDSON, W. F. 1984. The Meganos gorge and the geologic

- effects produced by compaction of the gorge fill. Pp. 37–51, in A. A. Almgren & P. D. Hacker (eds.), Paleogene Submarine Canyons of the Sacramento Valley, California Vol. 1. Pacific Section, American Association of Petroleum Geologists, Symposium.
- EISENBERG, L. I. & P. A. ABBOTT. 1991. Middle Eocene paralic facies, northern San Diego County, California. Pp. 55–72 in P. L. Abbott & J. A. May (eds.), Eocene Geologic History San Diego Region. Pacific Section, Society of Economic Paleontologists and Mineralogists, Book 68: Los Angeles, California.
- ELSIK, W. C. & J. E. BOYER. 1977. Palynomorphs from the middle Eocene Delmar Formation and Torrey Sandstone, coastal southern California. *Palynology* 1:173.
- FÉRUSAC, A. E. J. 1823. Monographie des espèces vivantes et fossiles du genre *Melanopsis* et observations géologiques à leur sujet. Mémoires de la Société d'Histoire Naturelle de Paris 1:132–164.
- FISCHER, P. H. 1880–1887. Manuel de Conchyliologie et de Paléontologie Conchyliologique ou Histoire Naturelle des Mollusques Vivants et Fossiles. Paris. 1369 pp., 23 pls.
- FOWKES, E. J. 1982. An Educational Guidebook to the Geologic Resources of the Coalinga District, California. West Hills College: Coalinga, California. 260 pp.
- FREDERICKSON, N. O. 1991a. Pulses of middle Eocene to earliest Oligocene climatic deterioration in southern California and the Gulf Coast. *Palaaios* 6:564–571.
- FREDERICKSON, N. O. 1991b. Age determinations for Eocene formations of the San Diego, California, area, based on pollen data. Pp. 195–199, in P. L. Abbott & J. A. May (eds.), Eocene Geologic History San Diego Region. Pacific Section, Society of Economic Paleontologists and Mineralogists, Book 68: Los Angeles, California.
- GABB, W. M. 1864. Description of the Cretaceous fossils. California Geological Survey, *Palaeontology* 1:57–243, pls. 9–32.
- GABB, W. M. 1868. An attempt at a revision of the two families Strombidae and Aporrhidae. *American Journal of Conchology* 4:137–149, pls. 13–14.
- GABB, W. M. 1869. Cretaceous and Tertiary fossils. California Geological Survey, *Palaeontology* 2:1–299, pls. 1–36.
- GIVENS, C. R. 1974. Eocene molluscan biostratigraphy of the Pine Mountain area, Ventura County, California. *University of California Publications in Geological Sciences* 109:1–107, pls. 1–11.
- GIVENS, C. R. 1994. Occurrence of the rare genus *Anapteris* (Bivalvia: Corbulidae) in the Eocene of California. *Journal of Paleontology* 68(1):168–171, fig. 1.
- GIVENS, C. R. & M. P. KENNEDY. 1976. Middle Eocene mollusks from northern San Diego County, California. *Journal of Paleontology* 50:954–975, pls. 1–4.
- GIVENS, C. R. & M. P. KENNEDY. 1979. Eocene molluscan stages and their correlation, San Diego area, California. Pp. 81–95 in P. L. Abbott (ed.), Eocene Depositional Systems, San Diego. Pacific Section, Society of Economic Paleontologists and Mineralogists: Los Angeles, California.
- HANNA, M. A. 1926. Geology of the La Jolla Quadrangle, California. *University of California Publications, Bulletin of the Department of Geological Sciences* 16:187–246, pls. 17–23.
- HANNA, M. A. 1927. An Eocene invertebrate fauna from the La Jolla Quadrangle, California. *University of California Publications, Bulletin of the Department of Geological Sciences* 16(8):247–398, pls. 24–57.
- HAQ, B. U. 1981. Paleogene paleoceanography: early Cenozoic oceans revisited. *Oceanologia Acta*. Pp. 71–82 in Proceedings of the 26th International Geological Congress, Geology of Oceans Symposium, Paris.
- HOUBRICK, R. S. 1988. Cerithioidean phylogeny. Pp. 88–128 in W. F. Ponder (ed.), *Prosobranch Phylogeny*. Malacological Review, Supplement 4.
- HOUBRICK, R. S. 1991. Anatomy and systematic placement of *Faunus* Montfort 1810 (Prosobranchia: Melanopsinae). *Malacological Review* 24:35–54.
- JESTES, E. C. 1963. A stratigraphic study of some Eocene sandstones, northeastern Ventura basin, California. Unpublished Ph.D. dissertation. University of California, Los Angeles. 253 pp.
- KEEN, A. M. & H. BENTSON. 1944. Check list of California Tertiary marine Mollusca. *Geological Society of America Special Papers* 56:1–280.
- KENNEDY, M. P. & G. W. MOORE. 1971. Stratigraphic relations of Upper Cretaceous and Eocene formations, San Diego coastal area, California. *The American Association of Petroleum Geologists Bulletin* 55(5):709–722.
- KEW, W. S. W. 1924. Geology and oil resources of a part of Los Angeles and Ventura Counties, California. *U.S. Geological Survey Bulletin* 753:1–202.
- LILLEGRAVEN, J. A. 1979. A biogeographical problem involving comparisons of later Eocene terrestrial vertebrate faunas of western North America. Pp. 333–347 in J. Gray & A. J. Boucrot (eds.), *Historical Biogeography, Plate Tectonics, and the Changing Environment*. Oregon State University Press: Corvallis, Oregon.
- LINNAEUS, C. 1758. *Systema Naturae, per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Tomus 1. Edition 10, Reformata Laurentii Salvii: Holmiae. 824 pp.
- LINK, M. H. 1975. Matilija Sandstone: a transition from deep-water turbidite to shallow-marine deposition in the Eocene of California. *Journal of Sedimentary Petrology* 45(1):63–78.
- LINK, M. H. & J. E. WELTON. 1982. Sedimentology and reservoir potential of Matilija Sandstone: an Eocene sand-rich deep-sea fan and shallow-marine complex, California. *The American Association of Petroleum Geologists Bulletin* 66(10):1514–1534.
- LOHMAR, J. M., J. A. MAY, J. E. BOYER & J. E. WARME. 1979. Shelf edge deposits of the San Diego embayment. Pp. 15–33 in P. L. Abbott (ed.), *Eocene Depositional Systems*. San Diego, California. Pacific Section, Society of Economic Paleontologists and Mineralogists: Los Angeles, California.
- MAY, J. A. & J. E. WARME. 1991. Marine sedimentology of the early to middle Eocene La Jolla Group. Pp. 73–88 in P. L. Abbott & J. A. May (eds.), *Eocene Geologic History San Diego Region*. Pacific Section, Society of Economic Paleontologists and Mineralogists, Book 68: Los Angeles, California.
- MERRIAM, C. W. & F. E. TURNER. 1937. The Capay middle Eocene of northern California. *University of California Publications, Bulletin of the Department of Geological Sciences* 24(6):91–114, pls. 5–6.
- MYERS, J. A. 1991. The early middle Eocene Torrey flora, Del Mar, California. Pp. 201–216 in P. L. Abbott & J. A. May (eds.), *Eocene Geologic History San Diego Region*. Pacific Section, Society of Economic Paleontologists and Mineralogists, Book 68: Los Angeles, California.
- NIEM, A. R., I.-C. RYU & W. A. NIEM. 1992. Geologic Interpretation of the Schematic Fence Diagram of the Southern Tye

- Basin, Oregon Coast Range. State of Oregon Department of Geology and Mineral Industries, Oil and Gas Investigation 18. 40 pp.
- NOVACEK, M. J. & J. A. LILLEGRAVEN. 1979. Terrestrial vertebrates from the later Eocene of San Diego County, California: a conspectus. Pp. 69–79, in P. L. Abbott (ed.), Eocene Depositional Systems, San Diego, California. Pacific Section, Society of Economic Paleontologists and Mineralogists: Los Angeles, California.
- NUTTALL, P. 1990. A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of northwestern South America. Bulletin of the British Museum, (Natural History), Geology Series 45(2):165–371, figs. 1–456.
- OLSSON, A. A. 1931. Contributions to the Tertiary paleontology of northern Peru: Part 4, the Peruvian Oligocene. Bulletins of American Paleontology 17(63):99–264, pls. 13–33.
- PETERSON, G. L. & P. L. ABBOTT. 1979. Mid-Eocene climatic change, southwestern California and northwestern Baja California. Palaeogeography, Palaeoclimatology, Palaeoecology 26:73–87.
- REDWINE, L. E. 1984. The Tertiary Princeton submarine valley system beneath the Sacramento Valley, California. Pp. 53–80 in A. A. Almgren & P. D. Hacker (eds.), Paleogene Submarine Canyons of the Sacramento Valley, California. Pacific Section, American Association of Petroleum Geologists, Symposium Vol. 1: Los Angeles, California.
- ROTH, B. 1988. Camaenid land snails (Gastropoda: Pulmonata) from the Eocene of southern California and their bearing on the history of the American Camaenidae. Transactions of the San Diego Society of Natural History 21(12):203–220, figs. 1–19.
- ROTH, B. 1991. Tropical “physiognomy” of a land snail faunule from the Eocene of southern California. Malacologia 33(1–2):281–288, figs. 1–12.
- ROTH, B. & T. A. PEARCE. 1988. “*Micrarionta dallasi*”, a helicinid (prosobranch), not a helminthoglyptid (pulmonate), land snail: paleoclimatic implications. The Southwestern Naturalist 33(1):117–119, fig. 1.
- ROUSH, K. A. 1986. Depositional environments of the Eocene Domengine Formation near Coalinga, Fresno County, California. Unpublished M.S. Thesis. California State University, Northridge. 99 pp.
- SAUL, L. R. 1983. Notes on Paleogene turritelas, venericardias, and molluscan stages of the Simi Valley area, California. Pp. 71–80 in R. L. Squires & M. V. Filewicz (eds.), Cenozoic Geology of the Simi Valley Area, Southern California. Pacific Section, Society of Economic Paleontologists and Mineralogists, Book 35: Los Angeles, California.
- SCHENCK, H. G. & A. M. KEEN. 1940. California Fossils for the Field Geologist. Preliminary edition. Stanford University: Stanford, California. 86 pp.
- SCHULEIN, B. J. 1993. Sedimentation and tectonics of the upper lower to lower middle Eocene Domengine Formation Vallecitos syncline, California. Unpublished M.S. Thesis. Stanford University. 343 pp.
- SPIX, J. B. & J. A. WAGNER. 1827. Testacea Fluvialia Brasiliensis. Munich. 36 pp., 29 pls.
- SQUIRES, R. L. 1984. Megapaleontology of the Eocene Lajas Formation, Simi Valley, California. Natural History Museum of Los Angeles County, Contributions in Science 350:1–76, figs. 1–19.
- SQUIRES, R. L. 1988a. Geologic age refinement of west coast Eocene marine mollusks. Pp. 107–112 in M. V. Filewicz & R. L. Squires (eds.), Paleogene Stratigraphy, West Coast of North America. Pacific Section, Society of Economic Paleontologists and Mineralogists, Vol. 58: Los Angeles, California.
- SQUIRES, R. L. 1988b. Rediscovery of the type locality of *Turritella andersoni* and its geologic age implications for west coast Eocene strata. Pp. 203–208 in M. V. Filewicz & R. L. Squires (eds.), Paleogene Stratigraphy, West Coast of North America. Pacific Section, Society of Economic Paleontologists and Mineralogists, Volume 58: Los Angeles, California.
- SQUIRES, R. L. 1991a. A new middle Eocene potamidid gastropod from brackish-marine deposits, southern California. The Veliger 34(4):354–359, figs. 1–5.
- SQUIRES, R. L. 1991b. Molluscan paleontology of the lower Eocene Maniobra Formation, Orocochia Mountains, southern California. Pp. 217–226, pls. 1–2, in P. L. Abbott & J. A. May (eds.), Eocene Geologic History San Diego Region. Pacific Section, Society of Economic Paleontologists and Mineralogists, Book 68: Los Angeles, California.
- SQUIRES, R. L. 1997. Taxonomy and distribution of the buccinid gastropod *Brachysphingus* from uppermost Cretaceous and lower Cenozoic marine strata of the Pacific slope of North America. Journal of Paleontology. 71(5):847–861, figs. 1–5.
- SQUIRES, R. L. & D. M. ADVOCATE. 1986. New early Eocene mollusks from the Orocochia Mountains, southern California. Journal of Paleontology 60(4):851–864, figs. 1–3.
- SQUIRES, R. L. & T. A. DEMERE. 1991. A middle Eocene marine molluscan assemblage from the usually nonmarine Friars Formation, San Diego County, California. Pp. 181–188, figs. 1–3 in P. L. Abbott & J. A. May (eds.), Eocene Geologic History San Diego Region. Pacific Section, Society of Economic Paleontologists and Mineralogists, Book 68: Los Angeles, California.
- SQUIRES, R. L. & J. L. GOEDERT. 1994a. New species of early Eocene small to minute mollusks from the Crescent Formation, Black Hills, southwestern Washington. The Veliger 37(3):253–266, figs. 1–29.
- SQUIRES, R. L. & J. L. GOEDERT. 1994b. Macropaleontology of the Eocene Crescent Formation in the Little River area, southern Olympic Peninsula, Washington. Natural History Museum of Los Angeles County, Contributions in Science 444:1–32, figs. 1–62.
- SQUIRES, R. L. & J. L. GOEDERT. 1995. New species of middle Eocene gastropods from the northern Doty Hills, southwestern Washington. The Veliger 38(3):254–269, figs. 1–18.
- SQUIRES, R. L. & J. L. GOEDERT. 1996. New species of small to minute gastropods of early Eocene age from the Crescent Formation, Black Hills, southwest Washington. The Veliger 39(3):226–240, figs. 1–32.
- SQUIRES, R. L., J. L. GOEDERT & K. L. KALER. 1992. Paleontology and stratigraphy of Eocene rocks at Pulali Point, Jefferson County, eastern Olympic Peninsula, Washington. Washington Division of Geology and Earth Resources, Report of Investigations 31:1–27, pls. 1–3.
- SQUIRES, R. L. & L. R. SAUL. 1997. Late Cretaceous occurrences on the Pacific slope of North America of the melanopsid gastropod genus *Boggsia* Olsson, 1929. The Veliger 40(3): 193–202, figs. 1–17.
- STEWART, R. B. 1927. Gabb's California fossil type gastropods. Proceedings of the Academy of Natural Sciences of Philadelphia 57:287–447, pls. 20–32.
- TODD, T. W. 1968. Paleoclimatology and the relative stability of

- feldspar minerals under atmospheric conditions. *Journal of Sedimentary Petrology* 38(3):832-844.
- TODD, T. W. & W. A. MONROE. 1968. Petrology of Domengine Formation (Eocene), at Potrero Hills and Rio Vista, California. *Journal of Sedimentary Petrology* 38(4):1024-1039.
- TRYON, G. W., JR. 1883. *Structural and Systematic Conchology: an Introduction to the Study of the Mollusca*. Vol. 2. Privately published. Philadelphia. 430 pp.
- TRYON, G. W., JR. 1885. *Manual of Conchology; Structural and Systematic, with Illustrations of the Species*. Vol. 7. Terebridae, Cancellariidae, Strombidae, Cypraeidae, Oculidae, Cassididae, Doliidae. Privately published. Philadelphia. 309 pp., 54 pls.
- TURNER, F. E. 1938. Stratigraphy and Mollusca of the Eocene of western Oregon. *Geological Society of America, Special Papers* 10:1-130, pls. 1-22.
- VOKES, H. E. 1939. Molluscan faunas of the Domengine and Arroyo Hondo formations of the California Eocene. *Annals of the New York Academy of Sciences* 38:1-246, pls. 1-22.
- WALSH, S. L., D. R. PROTHERO & D. J. LUNDOUIST. 1996. Stratigraphy and paleomagnetism of the middle Eocene Friars Formation and Poway Group, southwestern San Diego County, California. Pp. 120-154, in D. R. Prothero & R. J. Emery (eds.), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press: Cambridge.
- WARME, J. E. 1991. Delmar Formation and Torrey Sandstone as exposed along beach cliffs, Solana Beach, northern San Diego County. Pp. 39-54 in P. L. Abbott & J. A. May (eds.), *Eocene Geologic History San Diego Region*. Pacific Section, Society of Economic Paleontologists and Mineralogists, Book 68: Los Angeles, California.
- WEAVER, C. E. 1942[1943]. Paleontology of the marine Tertiary formations of Oregon and Washington. University of Washington, *Publications in Geology* 5 (Parts 1-3):1-789, pls. 1-104.
- WENZ, W. 1939-1944. *Gastropoda*. Teil 1: Allgemeiner Teil und Prosobranchia. Pp. 1-1639, figs. 1-4211, in O. H. Schindewolf (ed.), *Handbuch der Paläozoologie*, Band 6. Gebrüder Borntraeger: Berlin [reprinted 1960-1961].
- WOLFE, J. A. 1968. Paleogene biostratigraphy of nonmarine rocks in King County, Washington. U.S. Geological Survey Professional Paper 571:1-33.
- WOLFE, J. A. 1994. Tertiary climatic changes at middle latitudes of western North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 108:195-205.
- County, southwestern Oregon. White Tail Ridge formation (unknown member). Age: Middle early Eocene ("Capay Stage" but near the "Capay Stage"- "Domengine Stage" boundary). Collectors: D. W. Scharf & W. P. Popenoe, 3 September 1930; R. L. Squires, 10-11 July 1988. [= UCMP locs. A-661 & A-662].
- LACMIP 24258. Approximately at sharp bend in a short, paved road that leads from Highway 33 to Matilija Hot Springs, NE ¼ of the SE ¼ of section 29, T. 5 N, R. 23 W, U.S. Geological Survey Matilija Quadrangle, 7.5-minute, 1952 (photorevised 1967), Ventura County, southern California. Matilija Sandstone. Age: Early middle Eocene ("Transition Stage"). Collectors: E. C. Jestes, 1963; R. L. Squires, 1990 and 1996.
- SDSNH 3278. At 4760 Murphy Canyon Road, at elevation of 104 m (340 ft.) on W side of Murphy Canyon, 5746 m (18,850 ft.) S and 610 m (2000 ft.) E of NW corner of La Mesa Quadrangle, U.S. Geological Survey La Mesa Quadrangle, 7.5-minute, 1967, San Diego County, southern California. Upper part of Scripps Formation. Age: Early middle Eocene ("Transition Stage"). Collector: B. O. Riney, 23, February 1985. [A retaining wall now covers the collecting site].
- UCMP 3311. Information from Kew (1924:29): On point of ridge at edge of Simi Valley, south side of Simi Valley, 1.6 km (1 mi.) N and 0.13 km (0.08 mi.) W of SE corner of Piru quadrangle, Ventura County, southern California. Collector: B. L. Clark. Information from UCMP locality registry: Simi Hills, Simi Valley, Ventura County, southern California.
- UCMP 3586. At elevation of 99 m (325 ft.), on ridge immediately SE of Kellogg Creek, 302 m (990 ft.) N of NE corner of section 12, T. 1 S, R. 2 E, U.S. Geological Survey Byron Hot Springs Quadrangle, 7.5-minute, 1953 (photorevised 1968), Contra Costa County, northern California. Margaret Hamilton Sand [= division D of Meganos Formation as used by Clark & Woodford (1927)]. Age: Early Eocene ("Meganos Stage"). Collector: A. O. Woodford, circa 1920s.
- UCMP A-661. See LACMIP loc. 7206.
- UCMP A-662. Five meters stratigraphically higher than UCMP loc. A-661.
- UCMP A-1154. At elevation of 671 m (2200 ft.), on NE face of ridge marked by prominent red-sandstone capping on W side of Griswold Canyon, near center of W edge of section 23, T. 16 S, R. 10 E, U.S. Geological Survey Panoche Quadrangle, 7.5-minute, 1969, San Benito County, central California. Domengine Formation. Age: Late early to early middle Eocene ("Domengine Stage"). Collector: H. E. Vokes, 1930s.
- UCMP A-1547. Dark sandstone interbedded with basalt

LOCALITIES CITED

- CSUN 1450. About 225 m (836 ft.) W of junction of Highway 33 and a short, paved road that leads to Matilija Hot Springs, on S bank of North Fork Matilija Creek near W end of highway bridge that crosses the creek, NE ¼ of the SE ¼ of section 29, T. 5 N, R. 23 W, U.S. Geological Survey Matilija Quadrangle, 7.5-minute, 1952 (photorevised 1967), Ventura County, southern California. Matilija Sandstone. Age: Early middle Eocene ("Transition Stage"). Collector: R. L. Squires, 1990 and 1996.
- LACMIP 7206. On E bank of Little River just S of highway bridge over the river at Glide, SE ¼ of the NW ¼ of section 19, T. 26 S, R. 3 W, U.S. Geological Survey Glide Quadrangle, 15-minute, 1954, Douglas

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at base of sea cliff on small point about 183 m (600 ft.) due N of hill 108 on W side of Crescent Bay, approximately center of section 20, T. 31 N, R. 8 W, U.S. Geological Survey Joyce Quadrangle, 7.5-minute, 1950 (photorevised 1979), Clallam County, Olympic Peninsula, southwestern Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: S. A. Berthiaume & Mr. Bramkamp, 1935. [= UCMP loc. A-1548 (approximately) and UCMP loc. A-3212].

UCMP A-1550. About 30 m (100 ft.) S of small cove on W side of Crescent Bay and about 183 m (600 ft.) due E of hill 108 on W side of Crescent Bay, east central part of section 20, T. 31 N, R. 8 W, U.S. Geological Survey Joyce Quadrangle, 7.5-minute, 1950 (photorevised 1979), Clallam County, Olympic Peninsula, southwestern Washington. Crescent Formation. Age: Middle early Eocene ("Capay Stage"). Collectors: S. A. Berthiaume & Mr. Bramkamp, 1935.

UCR 4696. On U.S. Forest Service hiking trail from Fishbowls Campground to Pine Mountain Lodge, 396 m (1300 ft.) S and 122 m (400 ft.) W of NE corner of section 12, T. 6 N, R. 22 W, U.S. Geological Survey San Guillermo Quadrangle, 7.5-minute, 1943, Ventura County, southern California (Givens, 1974:97). Uppermost tongue of siltstone facies of Juncal Formation. Age: Early middle Eocene ("Transition Stage"). Collector: C. R. Givens, circa late 1960s.

UCR 4930. Light gray siltstone containing scattered pebbles and small cobbles, near base of sea cliff 120 m (394 ft.) S of end of beach access road in Blacks Canyon, 3.74 km (2.32 mi.) N, 7.66 km (4.75 mi.) E in zone 11 of UTM grid system, U.S. Geological Survey Del Mar Quadrangle, 7.5-minute, 1967, San Diego County, southern California. Ardath Shale. Age: Late early to early middle Eocene ("Domengine Stage"). Collector(s): Unknown.